

Fisheries Research 62 (2003) 53-63



www.elsevier.com/locate/fishres

# Life history strategies of striped bass, *Morone saxatilis*, populations inferred from otolith microchemistry

James A. Morris Jr. <sup>a,\*</sup>, Roger A. Rulifson <sup>a</sup>, Larry H. Toburen <sup>b</sup>

- <sup>a</sup> Department of Biology, East Carolina University, Greenville, NC 27858, USA
- <sup>b</sup> Department of Physics, East Carolina University, Greenville, NC 27858, USA

Received 31 January 2002; received in revised form 30 September 2002; accepted 30 September 2002

#### Abstract

Otolith microchemistry was used to investigate genetic, demographic and life history characteristics of striped bass, *Morone saxatilis*. Striped bass were collected from three river systems along the eastern seaboard: the Neuse River and Roanoke River, North Carolina, USA and the Stewiacke River, Nova Scotia, Canada. The elemental ratios Mn:Ca, Fe:Ca, Br:Ca, Zn:Ca, Cu:Ca and Sr:Ca were measured in otolith nuclei using broad-beam particle induced X-ray emission (PIXE) spectroscopy. Elemental ratios were not significantly different between several Roanoke River genotypes. Two dorsal coloration patterns found in Stewiacke River striped bass indicate the presence of ocean-going (green) and resident (black) contingents, but results of trace elemental analysis showed no differences in elemental signatures of otolith nuclei suggesting that the contingents originate from the same population. Observed Sr:Ca ratios were not stable between Roanoke River year classes; decreased levels of strontium found in 1 year class corresponded with a flooding event. Discriminant analysis using these six elemental ratios correctly identified approximately 88% of the Neuse River, 79% of Stewiacke River, and 47% of the Roanoke River striped bass to the river system from which they were caught during spawning activity. Misclassified individuals might be a result of environmental variability from subhabitats or represent wandering individuals from other populations. The Neuse River population, which is considered to be an endemic riverine population, had no obvious outliers. Results of this study show the increased power of information gathering provided by otolith microchemistry when used in concert with phenotypic and genotypic classification techniques.

© 2002 Elsevier Science B.V. All rights reserved.

Keywords: Otolith; Morone saxatilis; PIXE; Trace elements; Population discrimination

# 1. Introduction

The collection of information pertaining to life history and stock identification of fish is critical to making science-based regulatory decisions for promoting sustainable fisheries (Begg et al., 1999; Ihssen et al.,

1981). The prediction of future fish abundance and distribution relies on precise data related to fish population age structure, distribution, spawning habitats, and migratory patterns. For example, data pertaining to environmental conditions during early life can provide researchers with information necessary to protect nursery habitat (Gallahar and Kingsford, 1992; Milton et al., 1997; Thorrold et al., 2001). However, the management of a species whose habitat expands from freshwater to the marine environment has proven to be especially challenging throughout ontogeny. Tools

<sup>\*</sup> Corresponding author. Present address: National Oceanic and Atmospheric Administration, National Ocean Service, Beaufort, NC 28516, USA. Tel.: +1-252-728-8782; fax: +1-252-728-8784. *E-mail address:* james.morris@noaa.gov (J.A. Morris Jr.).

that provide researchers with information regarding all encountered habitats are critical in providing cumulative information during all of the transitional life stages.

For over two decades researchers have investigated the use of otoliths as internal markers, which provide a lifelong environmental record of ambient water properties (i.e., temperature, salinity, chemical composition) (Campana, 1999). Changes in ambient water characteristics result in changes of trace and minor elemental constituents of the calcified otolith matrix. By obtaining information relevant to ambient water properties, one can estimate migratory patterns and habitats encountered by a species at the individual, population or metapopulation level (Secor, 1999; Thorrold et al., 2001).

In some species, elemental strontium (Sr) concentrations in otoliths provide a strong indicator of temperature and salinity. Known correlations of strontium concentration with ambient water temperature and salinity (Radtke and Targett, 1984; Townsend et al., 1992; Secor et al., 1995; Kakuta et al., 1999) allow the reconstruction of ambient water temperatures and salinities encountered during otolith formation and growth (Townsend et al., 1995). These correlations may be positive or negative but they are specific to individual species (Kalish, 1989; Hoff and Fuiman, 1995; Bath et al., 2000) and can be affected by physiological changes and ontogenetic development of the individual (Hoff and Fuiman, 1993).

The analysis of other trace elements along with strontium provides an otolith "signature", potentially unique to a watershed or habitat, thus providing a tool for discriminating between populations. However, successful application of this technique hinges on knowledge of otolith elemental variability attributable to yearly changes, as yearly environmental conditions might not be stable over time thereby producing differences between year classes (Rooker et al., 2001).

Striped bass *Morone saxatilis* is a recreationally and commercially important species along the Atlantic Coast of North America (Rulifson and Dadswell, 1995). Furthermore, population densities have fluctuated over the past 100 years due in part to habitat loss, water quality degradation and stocking efforts. Striped bass populations north of Cape Hatteras, North Carolina, are anadromous and successful management

requires a comprehensive understanding of encountered habitats during both migration and spawning.

Past studies have investigated habitat utilization and population discrimination by employing various techniques such as tagging (Carmichael et al., 1998), genetic analysis (Sidell et al., 1980; Stellwag et al., 1994; Laughlin and Turner, 1996; Waldman et al., 1996), and phenotypic characterization. Tagging studies have provided data relevant to certain periods of life history. Genetic studies have been conflicting and in some cases inconclusive (Stellwag and Rulifson, 1995; Waldman and Wirgin, 1995). May (2001) explored the genetic heterogeneity (mtDNA) of one striped bass population—the Roanoke River—and identified three genotypes; however, investigation of these genotypes for life history differences is lacking.

Past striped bass research using otolith microchemistry to investigate estuarine migration and habitat utilization did not address the potential that differences in observed patterns might be a result of genetically distinct subgroups (Secor et al., 1995, 2001; Secor and Piccoli, 1996; Zlokovitz and Secor, 1999). If such groups exist, differences in life history and/or migratory patterns should be reflected in the otolith microchemistry as unique signatures.

The potential for resident and anadromous contingents of one population was investigated by Paramore and Rulifson (2001), who had noted unique dorsal coloration for striped bass overwintering in fresh water (black) and ocean (green) habitats prior to spring spawning in the Stewiacke River, Nova Scotia. Food habits and fatty acid analysis were used in combination with otolith microchemical analysis by LA-ICPMS and micro-PIXE to determine that habitat separation was a long-term pattern. Using a multi-way analysis, Gemperline et al. (2002) reexamined the otolith microchemistry data across year classes, and discovered that lifetime anadromy or residency was common, but some fish may switch at some point during life. Unfortunately, no genetic analysis was performed to determine whether these color morphs were different genetically.

The goal of this study was to ascertain whether adult and subadult striped bass retained otolith microchemistries in the primordium unique to natal watersheds and, if so, whether this could be used to investigate potential differences in migration and habitat utilization within a population relative to age class, phenotype, or genotype. Specific objectives were: (1) to obtain trace element signatures that reflect the juvenile phase of life history from the otoliths of adult striped bass from three unique watersheds; (2) to investigate microchemical variability among striped bass year classes within each population; (3) to determine whether otolith microchemical differences exist between known genotypes of one population; (4) to determine whether a population with two life history patterns—sea-going and resident had similar nursery habitat; (5) to determine whether the microchemistry of an otolith nucleus can be used to discriminate between striped bass populations of the North American Atlantic coast.

# 2. Site description

Three watersheds containing spawning striped bass populations were selected as models to explore the five study objectives (Fig. 1). The Neuse River, North Carolina (latitude 35.1°N) is a river system of moderate freshwater discharge that empties into the moderate salinity or mesohaline (5–15 ppt) Pamlico Sound estuary. The Neuse River population is considered to be relatively isolated from other striped bass populations. The Roanoke River, North Carolina (latitude 36.4°N), is a reservoir watershed that empties into the western part of Albemarle Sound. Albemarle Sound consists mostly of low salinity waters (0.5–5 ppt), but exhibits

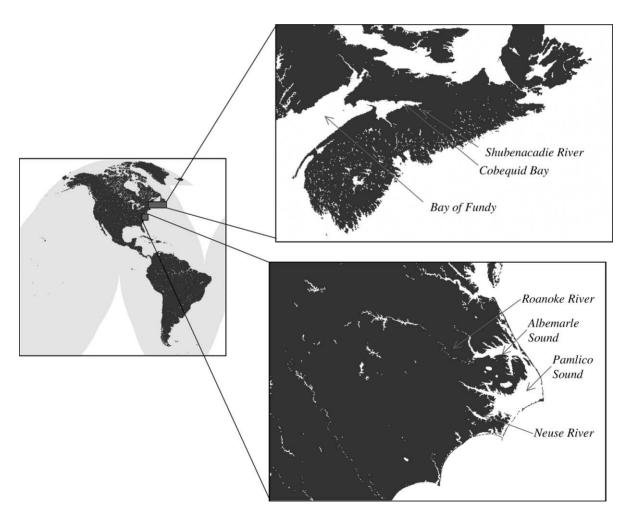


Fig. 1. Map depicting striped bass sampling locations and habitat.

higher salinity in the far eastern reaches near its connection with the Atlantic Ocean through Oregon Inlet. Adult striped bass wintering in coastal ocean waters off North Carolina have been tagged and released, with some individuals recaptured in the Albemarle Sound (Chapoton and Sykes, 1961; Wilson Laney, US Fish and Wildlife Service, Raleigh, NC, personal communication). Juvenile striped bass habitat is primarily the western side of Albemarle Sound (Taylor et al., 1992). The Stewiacke River, Nova Scotia (latitude 45°N), is a tributary to the Shubenacadie River, a tidal bore river system that experiences extreme changes in salinity (0-20 ppt), temperature, and tidal height (3 m) during saltwater intrusion from the Bay of Fundy (Rulifson and Tull, 1999). Rulifson and Dadswell (1995) suggested that juvenile Shubenacadie striped bass utilize the upper Bay of Fundy (likely Cobequid Bay) just seaward of the mouth of the Shubenacadie watershed as nursery habitat.

#### 3. Materials and methods

#### 3.1. Field collection

All striped bass were collected near or on the spawning grounds during spring prespawning migrations. All specimens had mature gonads in prespawn or postspawn condition. Sampling locations, dates, and number of fish sampled (n) include the Roanoke River, North Carolina, in 1999 (73), the Neuse River, North Carolina, in 2000 and 2001 (17), and the Stewiacke River, Nova Scotia in 1994 (47). Collections were made throughout the spawning season using gill net, electroshock, and rod and reel. Otoliths selected to examine otolith microchemical differences between Roanoke River genotypes were extracted from fish that were identified by May (2001) as belonging to Genotype I (n = 15), Genotype II (n = 6), or Genotype III (n = 5). Genetic classifications were identified using d-loop nucleotide substitution of mitochondrial DNA (May, 2001).

## 3.2. Otolith preparation for microanalysis

Sagittal otoliths were extracted, scrubbed to remove any surface tissue, cleaned with tap water, and stored in plastic and glass vials. Sagittae were embed-

ded in epoxy resin (Spurr) and allowed to polymerize at 21 °C for approximately 24 h. Following polymerization, embedded otoliths were mounted sulcus-side down to microscope slides with Crystal Bond 509 (Buehler, Inc.). Sagittae were then ground in the sagittal plane (distal surface) exposing the nuclear region using 400- and 600-grain wet silicon carbide sandpaper. To expose core increments (Secor et al., 1992). otoliths were given a final polish using 25 µm alumina paste (Buehler, Inc.) on a polishing machine (Crystal Master 6 Plus, Kingsley North, Inc.) equipped with a nylon PSA-backed polishing cloth (Buehler, Inc.). Each individual otolith was ultrasonically cleaned using ultrapure (Milli-Q) water for 5 min. Following sonication, otoliths were allowed to air dry in loosely capped vials for 12 h.

#### 3.3. Microanalysis

Particle induced X-ray emission (PIXE) spectroscopy has been used successfully to acquire otolith trace elemental concentrations for many species (Sie and Thresher, 1992; Kakuta et al., 1999; Halden et al., 2000). The use of standard or broad-beam irradiation was selected for this trace elemental analysis because of its ability to integrate the chemical information stored within the first annulus of the otolith (i.e., juvenile signature). A 2 MeV proton beam of approximately 1 mm diameter entered the otolith surface at normal incidence. X-rays were detected at 45° to the incident beam through a 0.1 mm aluminum absorber in order to attenuate Ca K lines, the most prominent line in the spectrum (Arai and Sakamoto, 1993). Proton beam intensity remained approximately 50 nA throughout the analysis. Precise target positioning was accomplished using a micro-positioning adjustment, which allowed for two-dimensional movement of the target relative to the beam spot. After analysis, accurate beam spot placement was confirmed by viewing the otolith under a dissecting microscope. If beam spot placement was inaccurate (i.e., less than 50% of beam spot centered on otolith nucleus), the otolith was reanalyzed (n = 14).

## 3.4. Spectrum analysis

The PIXE spectral intensities were analyzed using the Guelph PIXE software package (GUPIX)

(Maxwell et al., 1995), which extracts peak areas from a spectrum using a non-linear least-squares-fitting procedure. During each period of analysis, a standard (National Institutes of Standards and Technology, SRM-1c) was analyzed to obtain calibration parameters. X-ray yield measurements of Ca, Mn, Fe, Cu, Zn, Br and Sr were obtained. Some elements in some specimens were present at levels near the minimum detection limits; i.e., all elements were not homogeneously distributed throughout the population. To minimize bias, all fish were used regardless of whether the full complement of elements was present at detectable levels.

## 3.5. Aging analysis

Fish age was determined by sectioning the unused sagittae. Sagittae were mounted proximal side down on firm cardboard with Crystalbond 509 (Buehler, Inc.). With an isomet low speed saw (Buehler, Inc.), three dorso-ventral cross-sections were cut from the center of the otolith, with the middle section containing the otolith core. Sections were remounted on glass slides with Crystalbond 509 and viewed under a compound microscope with transmitted light. To enhance annuli visibility, some sections received a fine polishing using 25 and 0.3 µm alumina paste (Buehler, Inc.) on a polishing machine (Crystal Master 6 Plus, Kingsley North, Inc.) equipped with a nylon PSA-backed polishing cloth (Buehler, Inc). Where only one otolith was retrieved, scale annuli and whole otolith annuli were used to determine age. If the exact age was unclear, the fish was not used for the age class variability analysis. Ages for 129 Roanoke River and 15 Neuse River otoliths were determined and reader agreement was 97%. Aging comparisons between scales and otolith cross-sections for 115 Stewiacke River striped bass were determined previously by Paramore (1998) and reported as 90%. The techniques for removal and preparation of otolith cross-sections for aging (Paramore and Rulifson, 2001) were similar to those used for Roanoke River and Neuse River striped bass.

## 3.6. Statistical analysis

All otolith trace elemental data were tested for normality and homogeneity of variance. Two of the five

elemental ratios were not normally distributed; all data were normalized using arc-sin square root transformation. A one-way analysis of variance (ANOVA) pairwise comparison (Bonferroni) was used to compare differences between mean elemental ratios (P < 0.05 considered statistically significant). A multivariate ANOVA model (MANOVA, SAS Version 6.0) was used to assess accuracy of discriminating among populations (SAS Institute, 1996). Discriminant analysis (Seal, 1964), a classification method that measures the importance of factors determining membership within a category, was used to predict population discrimination accuracy between the three river systems using SYSTAT statistical computer software (Wilkinson, 1999).

#### 4. Results

Four of the five elemental ratios were stable between year classes for all three populations, but year class differences of Sr:Ca were observed for the Roanoke and Stewiacke populations. Roanoke striped bass otolith Sr:Ca ratios were significantly lower

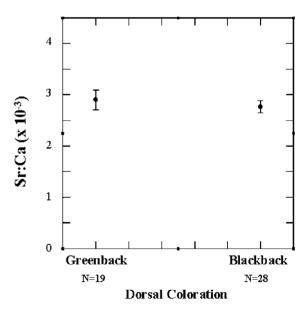


Fig. 2. Comparison of Sr:Ca ratios between greenback (sea-going) and blackback (resident) contingents of the Shubenacadie, NS watershed suggest that these subpopulations utilize similar nursery habitat. Error bars depict one standard error of the mean.

for the 1993 year class compared to the 1994, 1995 and 1996 year classes (d.f. = 4, 68; F = 6.209;  $P \le 0.008$ ); it was not different from the 1997 year class likely the result of small sample size. Stewiacke striped bass otoliths (1978, 1979, 1983, 1985, 1988, 1989, and 1990 year classes) also exhibited significantly different Sr:Ca (d.f. = 6, 40; F = 4.130; P = 0.013) and Mn:Ca ratios (F = 5.852;  $P \le 0.001$ ) between the 1985 year class (higher) and the 1988–1990 year classes (lower). By comparison, all mean elemental ratios of Neuse striped bass otoliths

were similar between the 1992, 1994, 1996, and 1998 year classes. There were no significant differences in the six elemental ratios by sex for any of the three populations.

Two of the striped bass populations, which have documented intrapopulation subgroupings, exhibited no substantial differences in otolith microchemistry between in-river subgroups. The three Roanoke genotypes, which were distributed randomly between year classes, had significant elemental differences only for the Cu:Ca ratio (d.f. = 2, 23; F = 5.676;  $P \le 0.015$ ).

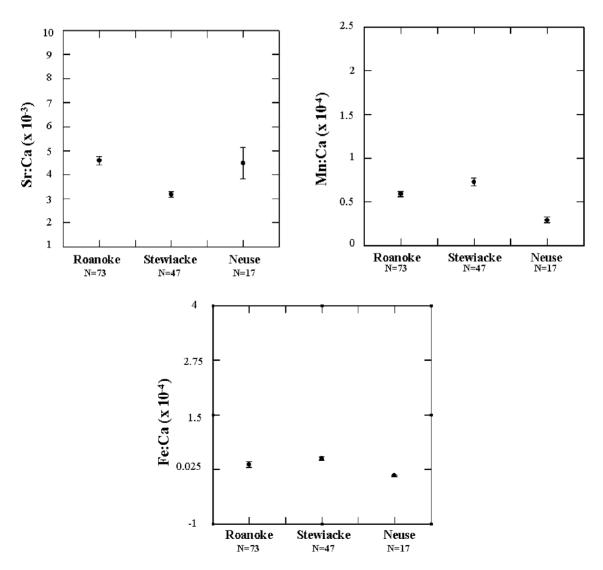


Fig. 3. Comparison of otolith Sr:Ca, Fe:Ca, and Mn:Ca ratios between river systems.

The Cu:Ca ratio was highest in Genotype III, and lowest in Genotype I. Stewiacke greenback (sea-going) and blackback (resident) striped bass exhibited statistically similar mean Sr:Ca ratios in the primordium (Fig. 2). The Zn:Ca ratio, which was higher in the black colored fish, was the only elemental ratio approaching statistical significance (d.f. = 1, 45; F = 3.946; P = 0.053).

Three elemental ratios were significantly different between the populations and were valuable contributors to successful classification of fish to the watershed of capture. The Sr:Ca ratio exhibited significant differences between the Roanoke and Stewiacke (P < 0.001) and Stewiacke and Neuse ( $P \le 0.009$ ) populations (Fig. 3). Mn:Ca ratios were significantly different between all three populations (P < 0.013), and Fe:Ca ratios were significantly different only between the Stewiacke and Neuse populations (P < 0.003) (Fig. 3). Trace elemental results were further explored between river systems using a two-way MANOVA. There was a significant multivariate effect for river location, Wilks lambda = 0.48, F(12, 258) = 9.32; P < 0.001. Using discriminant analysis, 88% of fish from the Neuse, 79% from Stewiacke, and 47% of Roanoke individuals were correctly classified to their natal river system (Fig. 4).

# Canonical Discriminant Functions

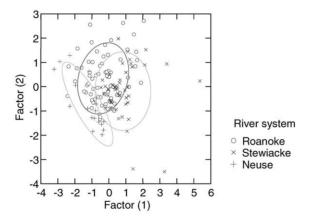


Fig. 4. Canonical plot scores and 68% confidence ellipses from discriminant analysis of the juvenile nucleus of adult striped bass otoliths from the Roanoke River, North Carolina, Neuse River, North Carolina and Stewiacke River, Nova Scotia. Discriminant analysis is based on six elements: Ca, Mn, Fe, Zn, Cu, and Sr.

#### 5. Discussion

Otolith elemental signatures can provide a powerful means of discriminating between populations and between spawning grounds or nursery habitats (Campana, 1999; Thresher, 1999). With broad-beam PIXE, measurements of elements deposited in the otolith during the initial months of first year growth are averaged; thus, the measured elemental signature reflects the juvenile habitat.

Aquatic and marine systems can experience great yearly dynamic changes in water chemistry (i.e., hurricanes, flooding, etc.) that can cause variability of otolith elemental signatures between year classes, so caution should be used when relying on 1 year class for otolith signature acquisition. Flooding may have been responsible for the significantly different Sr:Ca ratio of the Roanoke 1993 year class. Roanoke River water flow data, illustrated in Fig. 5, indicated significant flooding during the 1993 Roanoke River striped bass spawning period (15 April-30 June as defined by the North Carolina Wildlife Resources Commission). Direct cause for the decline of the Sr:Ca ratio is unclear, but potential causes might include temperature change (Radtke, 1989; Radtke and Morales-Nin, 1989; Townsend et al., 1992; Tzeng, 1994), salinity decrease (Secor and Rooker, 2000), or dietary and water chemistry changes (Gallahar and Kingsford, 1992).

One purported strength of determining Sr:Ca ratios is the potential to reconstruct striped bass juvenile nursery habitats in fresh waters, estuarine (mesohaline), or coastal (polyhaline) areas of watersheds. Laboratory experiments by Secor and Rooker (2000) provided evidence that strontium concentrations in adult striped bass otoliths increase with increased exposure to seawater. However, there may be additional environmental factors influencing strontium uptake that were not tested by Secor and Rooker because our results do not follow their paradigm.

The higher mean Sr:Ca ratio observed in Fig. 3 for the Roanoke striped bass suggests a higher salinity juvenile habitat for striped bass of the Roanoke River but this scenario is not likely. It is known from juvenile trawl and beach seine surveys conducted annually by the North Carolina Division of Marine Fisheries (NCDMF) that the greatest juvenile abundance is in the western reaches of Albemarle Sound (Taylor et al., 1992). Coutant and Benson (1987) hypothesized that

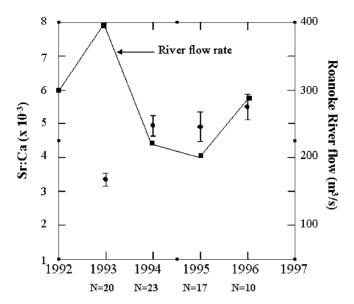


Fig. 5. Mean flow rates (m<sup>3</sup>/s) for the lower Roanoke River during the striped bass spawning period (15 April–30 June), and the corresponding striped bass Sr:Ca ratios in the otolith primordium by year class. Flow rate data was provided by the USGS gage just downstream of the Roanoke Rapids Dam at Rkm 210.

"habitat squeeze"—high water temperature and low dissolved oxygen conditions—that occur annually in Albemarle Sound might force juveniles from primary habitats in the Sound to secondary habitats of the 14 watersheds discharging into the Sound. If such a phenomenon exists, then this lateral movement could account for the relatively high variability of Sr concentrations of Roanoke River striped bass otoliths and thus the relatively poor classification for this population. However, the lateral movement by itself should not account for the relatively high Sr:Ca ratios observed for this population.

In a second case, the mesohaline Neuse River/Pamlico Sound estuary (Epperly and Ross, 1986) should result in higher levels of strontium in the otolith nucleus compared to Roanoke River striped bass otoliths. However, the average Sr:Ca ratios in otoliths of Neuse River striped bass were lower than Roanoke River striped bass otoliths.

In a third case, one would predict that striped bass utilizing the Shubenacadie-Stewiacke watershed would have the highest strontium levels of the three watersheds given the daily influence of ocean waters to the purported nursery area of Cobequid Bay hypothesized by Rulifson and Dadswell (1995). Studies

by Rulifson et al. (1987) and Rulifson and Dadswell (1995) found evidence of larvae in the most seaward reaches of the Shubenacadie watershed, and young of year fish <100 mm total length were collected from commercial fishing weirs in the inner Bay of Fundy in polyhaline conditions. In spite of this evidence, the low Sr:Ca ratios present in Shubenacadie-Stewiacke striped bass otoliths suggest that the nursery grounds are not downstream close to the mouth, but rather farther upstream in freshwater habitats. Furthermore, anecdotal evidence from commercial fishers assisting researchers in this watershed suggest that juvenile striped bass follow the tidal bore front during tidal exchanges and may reside in mid-reach fresher water areas of the watershed (R. Meadows, Stewiacke, Nova Scotia, personal communication).

Several possible explanations exist to explain why our results do not fit the Secor and Rooker paradigm. One possible reason is that striped bass nursery habitat estimations for each river system are incorrect, and juveniles exhibit far greater movements throughout the estuaries than previously thought. A more promising explanation is that laboratory experiments examined only temperature and salinity effects on strontium uptake, and did not consider all natural environmental

conditions that cause environmental stresses. For example, low dissolved oxygen concentrations, high temperatures, and low food availability could result in metabolic changes that influence the rate of uptake of certain trace and minor elements.

The statistical similarities of five of the six measured elements among genotypes of the Roanoke River provides evidence of early life history similarities. Given that Cu concentrations were near limits of detection during this analysis, further investigation is necessary to determine if Cu:Ca ratios are different between genotypes. May (2001) suggested that one subgroup, Genotype III, might exhibit resident behavior. Given that the current technique measured only the chemistry of the otolith nuclei, further analysis of the otolith from the nucleus to the outer edge (i.e., raster or line scan) using micro-PIXE (Halden et al., 1995; Campbell et al., 1999; Elfman et al., 2000; Halden et al., 2000; Paramore and Rulifson, 2001) might provide evidence of resident and anadromous differences between subgroups during the subadult and adult life stages.

Life history and migration differences between greenbacks and blackbacks of the Stewiacke River are believed to exist only after the first year of growth (Paramore and Rulifson, 2001). Analysis of the otolith nuclei resulted in similar elemental signatures between greenbacks and blackbacks, which supports the Paramore and Rulifson (2001) hypothesis that both color types utilize the same nursery habitat as juveniles. Decisions to exhibit resident or sea-going life history strategies could be driven by distinct contingents or genotypes, or may be simply a fortuitous event experienced by an individual fish (Gemperline et al., 2002). Further investigation of mtDNA might provide insight into the genetic structure of the Stewiacke population.

The ability to discriminate successfully between populations relies on the migratory habits of the population. The Neuse population exhibited the greatest discriminatory success, which can be attributed to the resident nature of the population and its isolation from other populations. The Stewiake population, which is an open population far removed from other spawning populations, was also successfully discriminated. However, wandering individuals not native to the population could compromise successful discrimination; the upper Bay of Fundy represents the northern ter-

minus of coastal migration for adult striped bass from anadromous populations at lower latitudes (Rulifson and Dadswell, 1995).

The ability to successfully discriminate Roanoke striped bass from the other two populations was impeded by the large variability in the elemental signature exhibited by this population. This variability might be the result of the large expanse of available oligohaline habitat, combined with thermal refugia provided by the 14 watersheds that discharge into Albemarle Sound. A contributing factor could also be introgression from other populations. It is known that a major offshore wintering ground for the coastal migratory stock is located in continental shelf waters between Virginia and Cape Hatteras (S.E. Winslow, North Carolina Division of Marine Fisheries, Elizabeth City, North Carolina, personal communication).

The application of otolith microchemistry accompanied by other population markers such as genetics could increase the accuracy of population discrimination. In many cases, genetic techniques alone cannot indicate sources of interpopulation variability. Future investigation of genetic variability assisted by otolith microchemistry might identify whether variability is associated with natural population subgroups, or caused by wandering fish from other populations (i.e., dissimilar juvenile otolith signature) or from stocking (same juvenile signature).

## 6. Conclusion

Otolith microchemistry has proven to be a strong and productive tool for gathering information about the life history of fish. Utilization of broad-beam PIXE for otolith nucleus signature acquisition provides the user with the ability to gather cumulative early life history information. Year class variability can complicate striped bass otolith microchemical signatures. Three genotypes of the Roanoke River striped bass population have similar elemental concentrations, which implies similar nursery habitat. Elemental analysis of Stewiacke River striped bass otolith nuclei revealed that ocean-going and resident contingents exhibit migration differences only after the first year of growth. The observed otolith microchemical variability of striped bass of the Roanoke River could be a result of variable estuarine habitats. Although

this yearly variability potentially undermines accurate discrimination between the striped bass populations of the North Atlantic Coast, two of the three populations from smaller watersheds had signatures distinctive enough to classify the fish with high accuracy. Further age specific analysis that integrates annual changes in otolith microchemistry could add additional insight into the migratory differences of these populations.

# Acknowledgements

We are grateful to Elisabeth Laban of the NOAA Beaufort Laboratory for her technical assistance with otolith preparation. We thank Pete Kornegay and Christian Waters (North Carolina Wildlife Resources Commission) for sampling assistance, and Don Holbert and Anthony Overton for statistical analyses. We also thank Lee Paramore and Paula May whose research preceded and contributed to this work. Jeffrey Govoni, Jonanthan Hare, John Waldman and an anonymous reviewer contributed valuable comments to improve this manuscript. The Institute for Coastal and Marine Resources and the Departments of Physics and Biology, East Carolina University, jointly supported this research.

## References

- Arai, N., Sakamoto, W., 1993. PIXE analysis of otoliths from reared red sea bream. Int. J. PIXE 3, 275–281.
- Bath, G.E., Thorrold, S.R., Jones, C.M., Campana, S.E., McLaren, J.W., Lam, J.H., 2000. Strontium and barium uptake in aragonitic otoliths of marine fish. Geochim. Cosmochim. Acta 64, 1705–1714.
- Begg, G.A., Friedland, K.D., Pearce, J.B., 1999. Stock identification and its role in stock assessment and fisheries management: an overview. Fish. Res. 43, 1–8.
- Campana, S.E., 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar. Ecol. Prog. Ser. 188, 263–297.
- Campbell, J.L., Babaluk, J.A., Halden, N.M., Kristofferson, A.H., Maxwell, J.A., Mejia, S.R., Reist, J.D., Teesdale, W.J., 1999. Micro-PIXE studies of char populations in northern Canada. Nucl. Instrum. Meth. B 150, 260–266.
- Carmichael, J., Haeseker, S., Hightower, J., 1998. Spawning migration of telemetered striped bass in the Roanoke River, North Carolina. Trans. Am. Fish. Soc. 127, 286–297.
- Chapoton, R.B., Sykes, J.E., 1961. Atlantic coast migration of large striped bass as evidenced by fisheries and tagging. Trans. Am. Fish. Soc. 90, 13–20.

- Coutant, C.C., Benson, D.L., 1987. Linking estuarine water quality and impacts on living resources: shrinking striped bass habitat in Chesapeake Bay and Albemarle Sound. Environmental Protection Agency, Office of Marine and Estuarine Protection, Environmental Sciences Division Publication No. 2972.
- Elfman, M., Limburg, K.E., Kristiansson, P., Svedang, H., Westin, L., Wickstrom, H., Malmqvist, K., Pallon, J., 2000. Complex life histories of fishes revealed through natural information storage devices; case studies of diadromous events as recorded by otoliths. Nucl. Instrum. Meth. B 161–163, 877–881.
- Epperly, S.P., Ross, S.W., 1986. Characterization of the North Carolina Pamlico-Albemarle Estuarine Complex. National Oceanic and Atmospheric Administration, Tech. Memo. NMFS-SEFC-175.
- Gallahar, N.K., Kingsford, M.J., 1992. Patterns of increment width and strontium: calcium ratios in otoliths of juvenile rock blackfish, Girella elevata (M.). J. Fish Biol. 41, 749–763.
- Gemperline, P.J., Rulifson, R.A., Paramore, L.M., 2002. Multi-way analysis of trace elements in fish otoliths to track migratory patterns. Chemom. Intell. Lab. Syst. 60, 135–146.
- Halden, N.M., Babuluk, J.A., Campbell, J.I., Teesdale, W.J., 1995. Scanning proton microprobe analysis of strontium in an arctic char, *Salvelinus alpinus*, otolith—implications for the interpretation of anadromy. Environ. Biol. Fish. 43, 333–339.
- Halden, N.M., Mejia, S.R., Babaluk, J.A., Reist, J.D., Kristofferson, A.H., Campbell, J.L., Teesdale, W.J., 2000. Oscillatory zinc distribution in Arctic char (Salvelinus alpinus) otoliths: the result of biology or environment? Fish. Res. 46, 289–298.
- Hoff, G.R., Fuiman, L.A., 1993. Morphometry and composition of red drum otoliths: changes associated with temperature, somatic growth rate, and age. Comp. Biochem. Physiol. A 106, 209– 219.
- Hoff, G.R., Fuiman, L.A., 1995. Environmentally induced variation in elemental composition of red drum (*Sciaenops ocellatus*) otoliths. Bull. Mar. Sci. 56, 578–591.
- Ihssen, P.E., Booke, H.E., Casselman, J.M., McGlade, J.M., Payne, N.R., Utter, F.M., 1981. Stock identification: materials and methods. Can. J. Fish. Aquat. Sci. 38, 1838–1855.
- Kakuta, I., Chiba, D., Ishii, K., Yamazaki, H., Iwasaki, S., Matsuyama, S., 1999. Population discrimination by strontium– calcium concentration rations of sagittal otoliths taken from the Japanese flounder *Paralichthys olivaceus*. Int. J. PIXE 9, 11–19.
- Kalish, J.M., 1989. Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. J. Exp. Mar. Biol. Ecol. 132, 131–178.
- Laughlin, T.F., Turner, B.J., 1996. Hypervariable DNA markers reveal high genetic variability within striped bass populations of the lower Chesapeake Bay. Trans. Am. Fish. Soc. 125, 49–55.
- Maxwell, J.A., Teesdale, W.J., Campbell, J.L., 1995. The Guelph PIXE software package II. Nucl. Instrum. Meth. B 95, 407–421.
- May, P.G., 2001. Genetic and morphological characterization of striped bass, *Morone saxatilis*, collected from the Roanoke River, North Carolina during the 1999 spawning season. Master's Thesis. East Carolina University, Greenville, NC.
- Milton, D.A., Chenery, S.R., Farmer, M.J., Blaber, S.J., 1997. Identifying the spawning estuaries of the tropical shad, terubok

- Tenualosa toli, using otolith microchemistry. Mar. Ecol. Prog. Ser. 153, 283–291.
- Paramore, L., 1998. Age, growth, and life history characteristics of striped bass, *Morone saxatilis*, from the Shubenacadie-Stewiacke River, Nova Scotia. Master's Thesis. East Carolina University, Greenville, NC.
- Paramore, L.M., Rulifson, R.A., 2001. Dorsal coloration as an indicator of different life history patterns for striped bass within a single watershed of Atlantic Canada. Trans. Am. Fish. Soc. 130, 663–674.
- Radtke, R.L., 1989. Strontium-calcium concentration ratios in fish otoliths as environmental indicators. Comp. Biochem. Physiol. A 92, 189–193.
- Radtke, R.L., Morales-Nin, B., 1989. Mediterranean juvenile bluefin tuna: life history patterns. J. Fish Biol. 35, 485–496.
- Radtke, R.L., Targett, T.E., 1984. Rhythmic structural and chemical patterns in otoliths of the Antartic fish *Notothenia larseni*: their application to age determination. Polar Biol. 3, 203–210.
- Rooker, J.R., Zdanowicz, V., Secor, D., 2001. Chemistry of tuna otoliths: assessment of base composition and postmortem handling effects. Mar. Biol. 139, 35–43.
- Rulifson, R.A., Dadswell, M.J., 1995. Life history and population characteristics of striped bass in Atlantic Canada. Trans. Am. Fish. Soc. 124, 477–507.
- Rulifson, R.A., Tull, K.A., 1999. Striped bass spawning in a tidal bore river: the Shubenacadie estuary, Atlantic Canada. Trans. Am. Fish. Soc. 128, 613–624.
- Rulifson, R.A., McKenna, S.A., Gallagher, M.L., 1987. Tagging studies of striped bass and river herring in upper Bay of Fundy, Nova Scotia. North Carolina Department of Natural Resources and Community Development, Division of Marine Fisheries, Morehead City, NC, ICMR Technical Report 87-02.
- SAS (Statistical Analysis Systems Institute, Inc.), 1996. SAS/STAT User's Guide, Version 6, vol. 2, 4th ed. SAS Institute, Cary, NC, USA.
- Seal, H.L., 1964. Multivariate Statistical Analysis for Biologists. Wiley. New York.
- Secor, D.H., 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fish. Res. 43, 13–34.
- Secor, D.H., Piccoli, P.M., 1996. Age- and sex-dependent migrations of striped bass in the Hudson River as determined by chemical microanalysis of otoliths. Estuaries 19, 778–793.
- Secor, D.H., Rooker, J.R., 2000. Is otolith strontium a useful scalar of life cycles in estuarine fishes? Fish. Res. 46, 359–371.
- Secor, D.H., Dean, J.M., Laban, E.H., 1992. Otolith removal and preparation for microstructural examination. In: Stevenson, D.K., Campana, S.E. (Eds.), Otolith Microstructure Examination and Analysis. Department of Fisheries and Oceans, Ottawa, Canada, pp. 19–57.
- Secor, D.H., Henderson-Arzapalo, A., Piccoli, P.M., 1995. Can otolith microchemistry chart patterns of migration and habitat

- utilization in anadromous fishes? J. Exp. Mar. Biol. Ecol. 192, 15-33
- Secor, D.H., Rooker, J.R., Zlokovitz, E., Zdanowicz, V.S., 2001. Identification of riverine, estuarine, and coastal contingents of Hudson River striped bass based upon otolith elemental fingerprints. Mar. Ecol. Prog. Ser. 211, 245–253.
- Sidell, B.D., Otto, R.G., Powers, D.A., Karwett, M., Smith, J., 1980. Apparent genetic homogeneity of spawning striped bass in the upper Chesapeake Bay. Trans. Am. Fish. Soc. 109, 99– 107
- Sie, S.H., Thresher, R.E., 1992. Micro-PIXE analysis of fish otoliths: methodolgy and evaluation of first results for stock discrimination. Int. J. PIXE 2, 357–379.
- Stellwag, E.J., Rulifson, R.A., 1995. Mitochondrial DNA stability and striped bass stock identification: response to comment. Trans. Am. Fish. Soc. 124, 956–959.
- Stellwag, E.J., Payne, E.S., Rulifson, R.A., 1994. Mitochondrial DNA diversity of Roanoke River striped bass. Trans. Am. Fish. Soc. 123, 321–334.
- Taylor, S.D., Henry, L.T., Winslow, S.E., 1992. North Carolina striped bass. Annual Progress Report, Project AFS-26, Segment 6. North Carolina Department of Environment, Health, and Natural Resources, Division of Marine Fisheries, Morehead City, NC, USA.
- Thorrold, S.R., Latkoczy, C., Swart, P.K., Jones, C.M., 2001. Natal homing in a marine fish metapopulation. Science 291, 297– 299
- Thresher, R.E., 1999. Elemental composition of otoliths as a stock delineator in fishes. Fish. Res. 43, 165–204.
- Townsend, D.W., Radtke, R.L., Corwin, S., Libby, D.A., 1992. Strontium: calcium ratios in juvenile Atlantic herring *Clupea harengus* L. otoliths as a function of water temperature. J. Exp. Mar. Biol. Ecol. 160, 131–140.
- Townsend, D.W., Radtke, R.L., Malone, D.P., Wallinga, J.P., 1995. Use of otolith strontium: calcium rations for hind-casting larval cod *Gadus morhua* distributions relative to water masses on Georges Bank. Mar. Ecol. Prog. Ser. 119, 37–
- Tzeng, W.N., 1994. Temperature effects on the incorporation of strontium in otolith of Japanese eel *Anguilla japonica*. J. Fish Biol. 45, 1055–1066.
- Waldman, J.R., Wirgin, I.I., 1995. Comment: Mitochondrial DNA stability and striped bass identification. Trans. Am. Fish. Soc. 124, 954–956.
- Waldman, J.R., Nolan, K., Hart, J., 1996. Genetic differences of three key anadromous fish populations of the Hudson River. Estuaries 19, 759–768.
- Wilkinson, L., 1999. Systat 9: Statistics I. SPSS Inc., Chicago, IL. Zlokovitz, E.R., Secor, D.H., 1999. Effect of habitat use on PCB body burden in Hudson River striped bass (*Morone saxatilis*). Can. J. Fish. Aquat. Sci. 56, 86–93.